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Original article

Timing of reproduction and association with environmental factors in female free-roaming dogs in southern India

H.R. Fielding[a*], A.D. Gibson[b,c,d], L. Gamble[b,d], K. A. Fernandes[e], I. Airikkala-Otter[e], I.G. Handel[a], B.M.de C. Bronsvoort[c], R.J. Mellanby[a], and S. Mazeri[a,c]

[a]The Royal (Dick) School of Veterinary Studies (R(D)SVS) and the Roslin Institute, Hospital for Small Animals, Easter Bush Veterinary Centre, Midlothian EH25 9RG, UK.
[b]Mission Rabies, 4 Castle Street, Cranborne, Dorset BH21 5PZ, UK.
[c]The Epidemiology, Economics and Risk Assessment (EERA) Group, The Roslin Institute and the Royal (Dick) School of Veterinary Studies (R(D)SVS), Easter Bush, Midlothian EH25 9RG, UK.
[d]Worldwide Veterinary Service, 4 Castle Street, Cranborne, Dorset BH21 5PZ, UK.
[e]WVS India, Gramya Bhavan/RDO-building complex, Aruvankadu, 643202 Nilgiris district, Tamil Nadu, India.
* Corresponding author. E-mail address: helen.fielding@ed.ac.uk (H.R. Fielding)

Abstract

Annual peaks in reproductive activity have been identified in multiple domestic dog populations. However, there is little evidence to describe how these peaks may be associated with environmental factors such as daylength, which plays a well-established role in breeding patterns of seasonally-reproductive species.

Data were collected from 2016–2020 during 7,743 and 4,681 neuter surgeries on adult female unowned free-roaming dogs in veterinary clinics in Goa and Tamil Nadu respectively. Temperature, precipitation, relative humidity, and daylength data were gathered for time periods preceding the neuter surgery that may have influenced the likelihood of pregnancy (potential influence periods). A multivariable generalised additive model was used to assess the relationship between these factors and pregnancy.

The prevalence of pregnancy varied by month in both locations indicating seasonality of reproduction in these groups. The annual pattern was more distinct in Goa with a peak in pregnancies between September and December. In Goa, decreasing daylength was associated with a higher probability of pregnancy ($p = 0.040$). Decreasing temperature was associated with decreasing probability of pregnancy in the Nilgiris ($p = 0.034$). Bitches had a median of 6 foetuses, with no evidence of seasonal variation.

Environmental factors were associated with patterns of pregnancy in free-roaming dogs, however statistically-significant factors varied by geographical location. Establishing local seasonal patterns of breeding in free-roaming dogs and assessing their relationship with environmental influences is recommended to facilitate effective and efficient population management strategies, which aim to reduce conflict between human and free-roaming dog populations.

Keywords: canine, population management, pregnancy, seasonality, stray dogs.

Introduction

The close relationship between humans and free-roaming domestic dogs (*Canis familiaris*) provides mutual benefits but can also lead to conflict (Tiwari et al., 2019). Transmission of zoonotic disease and bite injuries are common (Sudarshan et al., 2006) and some dog behaviours, such as barking and environmental contamination, can be disagreeable to humans (Srinivasan et al., 2019). Management of free-roaming dog populations can help to reduce these conflicts and thus safeguard the health and welfare of both species (Taylor et al., 2017). In order to effectively and efficiently manage these populations, we need to understand their demography. Since births are often a major driver of population growth, it is crucial to understand the the environmental factors that might influence their timing in free-roaming dog populations.

Canids are classed as monoestrous breeders (Concannon, 2011) as there is a fixed period when no oestrus occurs after each oestrus period (anoestrus), even if pregnancy does not occur. In domestic dogs, this anoestrus typically lasts around 7 months (England, 2010), but may be extended following pregnancy (Linde-Forsberg and Wallén, 1992; Mutembei et al., 2000). Unlike the rest of the *Canus* genus, the reproductive cycle of domestic dogs is considered non-seasonal and is not limited to a certain time of year (Concannon, 2011; England, 2010), putatively driven by selective pressures for increased fecundity, and the continuous availability of food (Lord et al., 2013). Despite this, annual peaks in reproductive activity have been identified in several free-roaming and confined populations (Table 1). In tropical climes, the surge in productivity of plants and animals after a rainy season has been posited to stimulate the onset of oestrus and subsequent pregnancies in wild canids (Lord et al., 2013). Change in photoperiod is also a possible driver of synchronisation, however there is conflicting evidence as to whether this process is active in domestic dogs (Fuller, 1955; Lord et al., 2013; see Table 1).

In regions where annual variation in daylength is more than 7 hours, three out of four studies identified found no evidence of seasonality in dogs kept in indoor environments with exposure to natural light (Canada - Bouchard et al., 1991, Sweden - Linde-Forsberg and Wallén, 1992; United Kingdom - Wigham et al., 2017), the remaining study detected reproductive seasonality in two groups of dogs in similar environments (Sweden - Bobic Gavrilovic et al., 2008). Eight out of nine studies identified in regions with annual variation in daylength of approximately 1–4 hours reported seasonality in free-roaming dogs (India - Chawla and Reece, 2002; Peru - Choy and Echevarría, 2005; Mexico - Ortega-Pacheco et al., 2007; India - Pal, 2003, 2001; India - Pal et al., 1998; India - Reece et al., 2008; India - Totton et al., 2010) and confined military dogs (Thailand - Chatdarong et al., 2007) whilst one paper detected no seasonality in free-roaming dogs where daylength varied by a similar period (South Africa - Morters et al., 2014). In one region with minimal annual change in daylength, seasonality was identified (Kenya - Mutembei et al., 2000), while in another region with the same daylength change seasonality was not detected (Indonesia - Morters et al., 2014). Thus, it seems the relationship between reproductive activity and daylength is not yet fully understood.

In these studies, seasonality has typically been determined by the presence of statistically-significant pairwise differences between months or seasons (excluding Choy and Echevarría, 2005 and Reece et al., 2008, Table 1), rather than direct assessment of climatic variables. An association between reproductivity and temperature and photoperiod has been reported in breeding German Shepherd dogs in Peru (Choy and Echevarría, 2005), but not yet assessed in terms of wider climatic variables or in free-roaming dog populations. To assess this relationship in free-roaming dogs, we collected data on pregnancy and foetus number during neutering surgeries performed in free-roaming, unowned dogs in Goa and the Nilgiri hills in Tamil Nadu, India from December 2016 to February 2020. We obtained data on key environmental factors; daylength, precipitation, humidity and temperature, during the study periods and combined them with temporal factors in a multivariable analysis to investigate their association with pregnancy in two free-roaming dog populations.

Methods

Study areas

Data was collected at two Worldwide Veterinary Service (WVS) international training centres in Goa and Tamil Nadu, India (Fig. 1). Tamil Nadu and Goa are states located in southern India. The literacy rate in the last census (2011) was 80.5% in Tamil Nadu and 88.5% in Goa, above the Indian average (Government of India: Ministry of Statistics & Programme Implementation, 2017) and infant mortality was lower than the Indian average, recorded in 2016 as 17 and 8 deaths per 1000 live births in Tamil Nadu and Goa respectively (Government of India, 2016). Tamil Nadu has a much larger geographical area (130,060 km^2) compared to Goa (3,702 km^2), one of the smallest states in India. In Tamil Nadu, the veterinary centre is located in the Nigiri hills where the climate is considered equatorial with dry winters, whereas Goa has an equatorial monsoon climate throughout (ESRI, 2011). The clinics provide neutering services for owned and unowned dogs in the local areas and both programmes were approved by the Animal Welfare Board of India and local government authorities. All surgeries in the Nigiris dataset and most surgeries in the Goa dataset (86%) were performed at the international training centres, the other Goa surgeries were performed at outreach clinics using the same protocols and WVS staff from the main clinic (Fig. 1). For brevity, we refer to this as the Goa dataset, though most dogs were concentrated in the northern part of the state (Fig. 1). Both clinics run all-year apart from a break in operations from late-December to early-January and in mid-July for the Nilgiris clinic. Both clinics are overseen by the WVS India management team. The number of male and female neuter surgeries performed in each region is described in Fig. S1. Ethics approval for this study was attained from the University of Edinburgh, Veterinary Ethics Research Committee (VERC 80.20).

Data collection

Each clinic employs teams of trained animal handlers to collect dogs. Dogs are typically caught using lightweight aluminium-framed butterfly nets, unless particularly amenable to handling (as outlined in Gibson et al., 2015). Catching teams do not actively select dogs and attempt to capture all dogs without a visible ear notch to signify the dog is already neutered. The GPS location of capture is recorded for each individual dog and they are assigned a unique number. Dogs are then transported to the clinic for surgery. A small number of unowned dogs are also brought to the clinic for surgery by members of the public. All surgeries were either performed or directly supervised by an experienced WVS veterinary surgeon. All surgeons use the same WVS surgical, anaesthetic, and analgesic protocols (as outlined in Airikkala-Otter et al., 2018). Information regarding age (juvenile, 4–11 months or adult, 12 months or over), pregnancy status at surgery (pregnant or non-pregnant), GPS collection location, and date of neuter surgery was recorded for each female dog onto the WVS data collection app (Gibson et al., 2018) by the vet assistant in consultation with the supervising WVS vet for that surgery. The vet assistants in the operating theatres at both clinics were consistent during the study period. The stage of gestation was not recorded, but bitches were defined as pregnant if visible sacculations of the uterine body and/or palpable foetuses were present at surgery, therefore the very earliest a pregnancy might have been detected would be at 20 days gestation (Concannon et al., 2001). After surgery, the dogs were returned to the GPS collection location, or to a safe point as close as possible to this location.

The study period in Goa was 1st December 2016–1st February 2020 and in the Niligiris 12th January 2017–25th March 2020. There was missing data on pregnancy status in Goa from June 11th–July 10th 2019 due to a missing question on a new version of the data collection form.

Mean latitude and longitude of GPS locations were calculated for each area and data on daylength (Thorsen, 2020), temperature, precipitation, and relative humidity (Copernicus Climate Change Service (C3S), 2018) were obtained. For the Nilgiris, satellite data were collected at North 11.38°, West 76.74°, South 11.37°, East 76.75° and for Goa, at North 15.59°, West 73.78°, South 15.58°, East 73.79°. Relative humidity was collected for specific air pressure related to the elevation at each clinic (Nilgiris = 775hPa at ~2242m above sea level, Goa = 1000hPa at ~ 60m above sea level).

Data analysis

The two sets of data were analysed separately using the same methods. Data were visualised as the proportion of female adult dogs pregnant and number of foetuses for pregnant dogs by month and by season (Goa - winter, summer, monsoon (heavy rain), and rainy; Nilgiris - winter, summer and rainy season). Mean pregnancy prevalence for each calendar month was calculated and differences between months were compared using the Pearson chi-squared test.

Influence periods

Environmental factors on the day of neutering itself are unlikely to describe patterns in pregnancy. Therefore, we have used lagged, summary co-variates to try to assess environmental conditions prior to the possible conception period. To determine the period of time during which environmental factors might influence pregnancy status; weather and daylength data were summarised for four potential 'influence' periods (50, 60, 75 and 100 days) prior to a possible range of conception dates based on the dog's surgery date. The time periods were selected to be broadly representative of the time period we might expect environmental factors to impact upon oestrus and pregnancy, based on reproductive seasonality in wild canids (Lord et al., 2013). A dog detected as pregnant at neutering in this study was at least 20 days pregnant, therefore influence periods were calculated from 20 days before neutering - the earliest date that a dog may have conceived. For example, if a dog was neutered on 20th April, the influence periods would be calculated 50, 60, 75 and 100 days back from 1st April corresponding to 11th February, 1st February, 17th January and 23rd December (in the previous year). If the dog was 20 days pregnant at neutering, the influence periods represent 50, 60, 75 and 100 days prior to conception. For dogs more than 20 days pregnant, the influence periods represent up to 43 days of the gestation period, and up to 7, 17, 32, and 57 days respectively prior to conception. The influence periods thus represent a range of days (7–50, 17–60, 32–75, and 57–100) prior to conception (Fig. 2), however, we henceforth refer to the upper limit of days for simplicity.

Summary of environmental factors

Weather variables were summarised during each influence period by calculating; i) the change in mean temperature and relative humidity using daily maximum and mean values from the first and last week of each influence period (16 variables), ii) the change in total precipitation from the first and last week of each influence period (4 variables) and iii) total precipitation from the entire influence period (4 variables). To summarise daylength, the change in daylength in minutes between the first and last days of each influence period (4 variables) and the daylength for the day of surgery were calculated (1 variable). All 29 variables were first run in univariable models with pregnancy as the binary response variable (Table S1). The option within each category (daylength, temperature, relative humidity, precipitation) associated with the lowest Akaike information criterion (AIC) (Burnham and Anderson, 2003) was selected as being the most appropriate influence period and variable combination to include in the multivariable model. To avoid collinearity in the final multivariable model, pairwise correlation coefficients were calculated between continuous variables. If over 0.8, the variable of the pair with the lower AIC in the univariable model was removed from the final model.

Final model

We used a multivariable generalised additive model to assess non-linear relationships between the binomial response variable (pregnant or non-pregnant) and the remaining temporal and environmental co-variates. Smooth terms were estimated using automatic selection of penalised regression in the R package ‘mgcv’ (Wood, 2011). Cross-validation was performed by training the model on each permutation of two years of data and testing on the remaining year using the R package ‘caret’ (Kuhn, 2020). To give an unbiased evaluation of modelling for the entire year, we only used years where full data was available (2017, 2018 and 2019). The area under Receiver Operating Characteristic (ROC) curves is reported using the R package ‘verification’ (NCAR - Research Applications Laboratory, 2015). This analysis was performed for each study area separately due to environmental differences between the two geographical areas. All data processes were performed in R (R Core Team, 2018) and ‘ggplot2’, ‘tidyverse’, and ‘rsample’ were used for data manipulation and plots.

Results

Reproduction

Of the 7743 adult female free-roaming dogs that were submitted for neutering in Goa from December 2016 to February 2020, 7.7% (n = 593) were identified as pregnant during surgery. Monthly pregnancy prevalence showed statistically-significant variation between aggregated monthly proportions (Pearson’s chi-squared = 120.52, p < 0.01). The proportion of female dogs pregnant per month ranged from 2.5–20.7% (mean = 8.4%, SD = 4.1%) and was increased from September to December (Fig. 3).

In the Nilgiris, 4681 adult female free-roaming dogs were submitted for neutering between January 2017 and March 2020 and 8.8% were identified as pregnant during surgery (n = 414). Monthly aggregated pregnancy prevalence showed statistically-significant variation between months

(Pearson's chi-squared = 28.35, $p = 0.003$), with increased proportions of pregnant dogs from July to December. However, there was less variation between months (mean = 8.9%, SD = 3.4%, range = 2.8–15.2%, Fig. 3), compared to Goa.

Environmental factors

Annual change in daylength was greater in Goa (110.3 minutes) than in the Nilgiris (81.7 minutes; Fig. 1). Mean annual temperature was higher in Goa (mean = 27.0°C, SD = 0.1°C) compared to the Nilgiris (mean = 21.6°C, SD = 0.3°C; Fig. 1). Mean annual relative humidity values were similar (Goa: mean = 75.8%, SD = 0.5%, Nilgiris: mean = 71.2%, SD = 1.6%; Fig. 1) with the most humid part of the year from June to August. From 2016 to 2019, mean annual precipitation was greater in Goa (2838 mm, SD = 551 mm; Fig. 1), which experienced a shorter, more intense monsoon season (June-September), compared to the Nilgiris (1683 mm, SD = 283 mm; Fig. 1).

Univariable selection process

Environmental summary variables selected for the final model varied between datasets (Table S1). The 100-day influence period was selected in all but one category in the Nilgiris data (total precipitation was 60 days). In Goa, the change in daylength 50 days before conception was most informative compared to other time periods, then changes in relative humidity and temperature were summarised over 60 and 100 days respectively.

Due to high negative correlation between precipitation and daylength in Goa ($r^2 = -0.82$, $p < 0.001$, Fig. S2), total precipitation over 100-day influence period was removed from the final model. No other pairs of variables were correlated over the threshold value (Fig. S2), therefore they were all included in the final models.

Final models

Both models reported statistically-significant non-linear relationships between the proportion of pregnant dogs and the day of year, providing evidence for annual variation of pregnancy in these regions (Table 2). For both regions, the highest probability of pregnancies was around day 200 to 250 (~19th July to 7th September). This relationship was more evident in the Nilgiris dogs but this parameter also had greater uncertainty (Fig. 4). The proportion of pregnant dogs in the Nilgiris was stable for the first half of the study, then declined; whereas the Goa population showed an initial decrease, then increase later in the study period (Fig. 4).

In Goa, there was an increasing probability of pregnancy associated with decreasing daylength during the influence period (Fig. 4). In comparison, increasing daylength during the influence period was associated with a consistently lower chance of pregnancy (Fig. 4). Change in daylength was not statistically-significantly associated with pregnancies in the Nilgiris population (Table 2).

In the Nilgiris, decreasing temperature was statistically-significantly associated with a decreasing risk of pregnancy, whereas, stable and moderate increases in temperature were associated with a more constant increased risk of pregnancy (Fig. 4). Greater increases in temperature (over 3°C) in the 100-day influence period were again associated with a slightly decreasing risk of pregnancy (Fig. 4). In Goa, no weather variables were statistically-significantly associated with pregnancy (Table 2).

Results of cross-validation between years showed reasonable and consistent predictive performance of the Goa model (0.57–0.64; Table S2), but poorer, yet consistent predictive capacity in the Nilgiris model (0.49–0.54; Table S2).

Foetal numbers were recorded for 89.0% (n = 528) and 98.8% (n = 409) of pregnant dogs in Goa and the Nilgiris respectively. The median number of foetuses in pregnancies from Goa and the Nilgiris was 6 (interquartile range = Goa 5–7; Nilgiris 4–7). There was no visible seasonality or trend to the number of foetuses (Fig. 5).

Discussion

Our study has revealed that environmental factors prior to conception were associated with prevalence of pregnancies in our two study populations. Despite the same methods and analysis, these effects varied between the two populations suggesting that seasonality of reproduction is influenced by different environmental factors at a local scale.

In both study populations, we found evidence for a concentration of pregnancies occurring at certain times of the year (Goa - September to December, Nilgiris - July to December). This period was more distinct in Goa, where the delineation of seasons is also clearer; with a distinct period of heat, building up to a monsoon, followed by a cooler period. In contrast, the Nilgiri hills at a higher elevation, experience a more equable climate, with cooler temperatures and less rain. Comparable studies in free-roaming dogs in India show a similar synchronisation of pregnancies during the post-monsoon period from September to December (Chawla and Reece, 2002; Reece et al., 2008; Totton et al., 2010). Boosts in productivity following heavy rains have been suggested as drivers of seasonal reproduction in wild canids. However, unlike their wild ancestors, free-roaming domestic dogs tend to be heavily reliant on human activities for their food. Therefore, the relationship between environmental factors and reproduction may be direct, but also could be mediated through changes in human activity, e.g. an increase in human activity after a monsoon season.

In the Nilgiris, more pregnancies were associated with stable and moderate increases in temperature during the influence period of 57–100 days before conception and fewer pregnancies were associated with decreases or greater increases in temperature (>3°C difference). This might indicate that stable ambient temperatures are more favourable conditions for pregnancies in this region, avoiding lower temperatures which may place greater metabolic demand on the dogs (Mussa and Prola, 2005; Schäfer and Hankel, 2020). A similar effect of fewer pregnancies in times of relatively more extreme climatic conditions was reported in stray dogs in Mexico, where pregnancies were most likely in the warm-humid season compared to the warm-dry or fresh-humid seasons (Ortega-Pacheco et al., 2007), and extreme temperatures have been shown to alter timing of reproduction in other mammals (Bronson, 1985; Rödel et al., 2005).

In addition to the day of year effect, decreasing daylength in the 7–50 days prior to conception was associated with more pregnancies in Goa, which aligns with the physiological process in wild canids, which are reported to be short-day breeders (Lord et al., 2013). Located further south, the dogs in the Nilgiris experienced a narrower range of daylength, which might account for daylength being less informative. Although the difference in annual change in daylength is relatively small, unlike previous work, this study may be better-placed to detect such an effect due to direct assessment of changes in daylength and replicated methods in clinics, data collection, analysis, and similarities in the study populations, i.e. free-roaming dogs in southern India.

The number of foetuses was consistent throughout the study, providing more robust evidence for seasonal stability and consistency in the number of foetuses detected in free-ranging Indian dogs during gestation (Chawla and Reece, 2002; Pal et al., 1998; Totton et al., 2010).

Although three full years of data is comparable to many previous studies into the seasonality of reproduction, we note that making predictions about trends over time would benefit from a longer-term dataset, which the authors plan to generate over time. Using a GAM framework rather than a time-series analysis, allowed more flexibility in the model across different time periods.

The physiological mechanism of seasonality of reproduction in domestic dogs is unclear and we did not collect data regarding stage of gestation, therefore our influence periods are associated with some uncertainty. The influence periods selected for the final models encompass the range of possible influence periods provided to the models, perhaps suggesting that due to the overlap in the influence periods available to the model, the small differences between influence periods were not so important in the prediction of pregnancies.

The results of this study suggest that neutering campaigns might prove most effective if intensively aimed between August and December in Goa, before and during the period of peak pregnancies.

Neutering campaigns in the Nilgiris however, may take advantage of the extended seasonal nature of pregnancies and concentrate neutering in the latter half of the year – from June to December. Neutering before the period of peak pregnancies has the dual benefit of reducing the number of unwanted puppies born into the population, thereby reducing the suffering due to the high mortality rate in puppies (Pal, 2001) and potentially reducing the number of surgeries that need to be performed in the future as part of dog population management initiatives. Dog population management models tend to focus on the intensity or rate of population control (Kisiel et al., 2018; Santos Baquero et al., 2016), rather than the time of year or season at which the intervention occurs. The authors of this study plan future modelling studies that will quantitatively assess the performance of neutering strategies targeted in different seasons relative to the degree of seasonality identified in that population, enabling robust, evidence-based recommendations for future strategies.

Domestic dogs are one of the most flexible and adaptive species, able to survive and thrive in a range of environments. Human interventions can result in complex demographics that vary among geographical locations and cultures. Our study suggests that free-roaming dog populations, even within the same country, show differences in the annual pattern of pregnancies, which might impact upon the effectiveness of neutering programmes. Strategies for population management are likely to be more effective if they are tailored to a particular region, considering the local dog ecology.

Conflict of interest

None of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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Supplementary materials

Supplementary information associated with this article can be found in the online version at doi: …

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Table 1

Summary of published papers reporting temporal patterns in pregnancy and oestrus periods in domestic dog populations worldwide. Koppen climate classification was based on reported study locations and approximate daylength is derived from timeanddate.com (Thorsen, 2020).

Authors and year of publication	Breed of dog	No. of bitches	Study period	Controlled breeding?	Reproductive parameter	Method of detection	Was statistically-significant annual variation detected (method)?	Climate	Location	Annual change in daylength	Environment
Totton et al., 2010	Local breed	5400	2007	No	Oestrus and pregnancy	Surgical identification	Yes - peak in September to December (chi-squared test)	Dry	Jodhpur, India	2 hours 58 minutes	Free-roaming
Reece et al., 2008	Local breed	~25000	1995-2006	No	Pregnancy	Surgical identification	Yes - peak September to December (maximum likelihood estimate)	Dry	Jaipur, India	3 hours 23 minutes	Free-roaming
Chawla and Reece, 2002	Local breed	8121	1996-2000	No	Oestrus (n = 7115) and pregnancy (n = 8121)	Surgical identification	Yes - peak August to December (chi-squared test)	Dry	Jaipur, India	3 hours 23 minutes	Free-roaming
Wigham et al., 2017	Mainly LR and GR, retriever crosses, some GSDs.	568	2005–2014	Yes	Oestrus	Retrospective records	No (visual inspection of plots, non-parametric regression, and autocorrelation analysis)	Temperate	United Kingdom	9 hours 8 minutes	Home environment
Morters et al., 2014	Local breeds	~1111	2008–2011	No	Oestrus and pregnancy	Observation	No - (visual inspection of plots and autocorrelation analysis)	Tropical	Bali, Indonesia	59 minutes	Owned, free-roaming
						Observation		Temperate	Johannesburg, South Africa	3h 17 minutes	

Authors and year of publication	Breed of dog	No. of bitches	Study period	Controlled breeding?	Reproductive parameter	Method of detection	Was statistically-significant annual variation detected (method)?	Climate	Location	Annual change in daylength	Environment
Chatdarong et al., 2007	Dobermann, GSD, LR, Rottweiler.	53	1998–2004	Yes	Oestrus and whelping	Observation	Yes - whelping was significantly lower in April – June, but oestrus was not significantly different between months or seasons (ANOVA analysis)	Tropical	North-East Thailand	1 hour 37 minutes	Separately in wire cages with free access to outdoor runs
Bobic Gavrilovic et al., 2008	Drever (scent hound)	1665	1995–2006	Yes	Successful mating and whelping dates	Retrospective records from owner	Yes - more whelpings in winter and spring (chi-squared test)	Continental	Sweden	Ranges from 10 hours 25 minutes in South to 24 hours in far North	Mostly home environment
		113				Retrospective records	Yes - more matings and whelpings in winter and fewer in summer (chi-squared test)	Temperate	Sätila, Sweden	11 hours 28 minutes	Individual pens with runs
Ortega-Pacheco et al., 2007	Local breeds	300	2003	No	Oestrus and pregnancy	Post-mortem examination	Yes - fewest pregnancies in the warm-dry season but no significant variation in oestrus periods (ANOVA and logistic regression)	Tropical/ Dry	Meridia, Mexico	2 hours 33 minutes	Free-roaming

Authors and year of publication	Breed of dog	No. of bitches	Study period	Controlled breeding?	Reproductive parameter	Method of detection	Was statistically-significant annual variation detected (method)?	Climate	Location	Annual change in daylength	Environment
Choy and Echevarria, 2005	GSD	300	1997–2000	Yes	Oestrus	Breeder records	Yes - more pregnancies March to July and related to photoperiod and temperature (multivariable linear regression)	Dry	Lima, Peru	1 hour 25 minutes	Breeder environment
Pal et al., 2003	Local breed	10	1997–2000	No	Mating and oestrous	Observation	Yes, all mating occurred on September to November and peaked in October	Tropical	Bhabanibera, West Bengal, India	2 hours 51 minutes	Free-roaming
Pal et al., 2001	Local breed	112	1994–1998	No	Mating and sighting of puppies	Observation	Yes - matings highest in October, births highest in December and January (chi-squared test)	Tropical	Katwa, West Bengal, India	2 hours 55 minutes	Free-roaming
Pal et al., 1998	Local breed	64 litters	1993–1996	No	Sighting of puppies	Observation	No - Peak in births October to January but no statistical analysis	Tropical	Katwa, West Bengal, India	2 hours 55 minutes	Free-roaming
Mutembei et al., 2000	GSD	594	1982–1997	Yes	Oestrus and whelping dates	Retrospective breeder records	Yes - oestrus periods highest in October, and lowest in April (t-test)	Tropical/Dry	Kenya	9 minutes	Owned: unknown
Linde-Forsberg et al., 1992	GSD, LR	36, 20	Not stated	Yes	Oestrus	Retrospective records	No (chi-squared test)	Continental	Sollefteå, Sweden	15 hours 47 minutes	Home environment

Authors and year of publication	Breed of dog	No. of bitches	Study period	Controlled breeding?	Reproductive parameter	Method of detection	Was statistically-significant annual variation detected (method)?	Climate	Location	Annual change in daylength	Environment
Linde-Forsberg et al., 1992	Beagles	36	Not stated	Unclear	Oestrus	Retrospective records	Yes - oestrus periods highest in May–July (chi-squared test)	Continental	Sollefteå, Sweden	15 hours 47 minutes	Housed as a colony with access to outdoors
Bouchard et al., 1991	Maltese, Yorkshire, Lhasa Apso, Bouvier des Flandres	19	1985–1988	Yes	Oestrus and pregnancy	Retrospective records	No - variation not consistent between years (chi-squared test)	Continental	St-Hycinthe, Quebec, Canada	7 hours 20 minutes	Indoors, constant 22˚C
	Beagles	48									
Christie and Bell, 1971	Multiple (40) pedigree breeds	449	1969	Yes	Oestrus	Retrospective questionnaire	Yes – more oestrus periods February–May than October–January (ANOVA)	Temperate	England and Wales	12 hours 6 minutes (north) - 8 hours 17 minutes (south)	Breeder environment
Engle, 1946	Cocker spaniel, great dane, setters, pekingese.	3754	1942–1943	Yes	Whelping	Retrospective breeder records	No - whelping was uniform throughout the year (no statistical analysis)	Dry, Temperate, Continental	United States	7 hours 34 minutes (north) - 3 hours 13 minutes (south)	Home environment

LR = labrador retriever, GR = golden retriever, GSD = German Shepherd

Table 2

GAM logistic regression analysing the relationship between pregnancy and environmental and temporal factors in adult, free-roaming dogs in Goa (n = 7743) and the Nilgiri hills, India (n = 4681).

Co-variate	**Effective degrees of freedom**	**Ref. degrees of freedom**	**Chi-squared statistic**	***P* value**
Goa				
Day of study	3.06	3.71	12.95	0.015
Day of year	1.24	8.00	5.01	0.013
Change in daylength (mins) over 50-day influence period	2.69	3.30	8.87	0.040
Change in mean relative humidity (%) from mean of first and last week of 60-day influence period	2.13	2.70	6.95	0.094
Change in maximum temperature (℃) from mean of first and last week of 100-day influence period	1.00	1.00	1.09	0.296
Nilgiris				
Day of study	2.16	2.66	9.40	0.027
Day of year	1.16	10.00	2.64	0.045
Change in daylength (mins) over 100-day influence period	2.77	3.46	3.41	0.551
Total precipitation (mm) in 60-day influence period	2.50	3.13	3.94	0.326
Change in mean temperature (℃) between mean of first and last weeks of 100-day influence period	2.41	3.00	8.68	0.034
Change in mean relative humidity (%) from mean of first and last weeks of 100-day influence period	1.00	1.01	0.32	0.574

Figure legends

Figure 1

Location and summary climate parameters for study sites in Goa and the Nilgiri Hills in Tamil Nadu, India. Left-side map indicates the GPS pick-up locations of free-roaming dogs neutered in the study. Right-side plots show monthly mean daylength, precipitation, relative humidity, and temperature (points) with standard deviation (error-bars) from 2016–2019. Base map images are the intellectual property of Esri and is used herein under license. Copyright © 2019 Esri and its licensors. All rights reserved.

Figure 2

Schematic to show estimation of putative influence periods for reproductive seasonality. As pregnancies less than 20 days are not detectable at surgery and stage of gestation was not recorded, we estimate that all recorded pregnancies are between 20 and 43 days. This means influence periods in the study represent a range of time periods. If a bitch was neutered on day 20 of gestation, the influence periods represent 50, 60, 75, and 100 days pre-conception, whereas for a bitch neutered later in pregnancy, the influence periods may represent up to 43-days during gestation, plus up to 7, 17, 32, and 57 days pre-conception respectively. Therefore for any given dog in the study the influence periods might represent 7–50, 17–60, 32–75, and 57–100 days preconception.

Figure 3

Monthly proportion of adult female free-roaming dogs that were pregnant at neutering in Goa clinic from December 2016 to February 2020 (left) and the Nilgiris clinic from January 2017 to February 2020 (right). Background colours indicate approximate season in each region, dark blue = monsoon, light blue = rainy (less rain than monsoon), orange = summer, yellow = winter.

Figure 4

Relationships between probability of pregnancy and temporal and environmental co-variates. Data from generalised additive models using data from study areas in Goa (top panel) and the Nilgiri hills (bottom panel). Temporal co-variates in both models are day of study (converted to numeric and /1000) and day of year. Environmental co-variates in the Goa model are change in daylength (mins) from start to end of 50-day influence period (IP), change in mean relative humidity between the mean of the first and last week in 60-day IP, and the change in maximum temperature between the mean of the first and last week in a 100-day IP. Environmental co-variates in the Nilgiris model are change in daylength (mins) from start to end of 100-day IP, change in mean temperature from mean of first and last weeks of a 100-day IP, change in mean relative humidity from mean of first and last weeks of a 100-day IP, and total precipitation in 60-day IP. Values are reported in Table 2.

Figure 5

Temporal distribution of number of foetuses recorded in 937 free-roaming adult female dogs from December 2016 to February 2020 with glm smooth function applied (‘ggplot2’ R package; left panel) and summary distribution of foetus numbers (right panel) for both study regions; Goa (yellow) and the Nilgiri Hills (green), India.